PATTERNS OF POSTFIRE REGENERATION IN A SOUTHERN CALIFORNIA MIXED CHAPARRAL COMMUNITY

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Abstract

Effects of prefire stand age, fire intensity, and hillslope position on postfire vegetation recovery during the first two postfire seasons were studied in two contrasting stands of mixed chaparral at San Diego State University's Sky Oaks Field Station (San Diego County, CA). One stand was approximately 60-years old and the other 12-years old when both burned in the July 2003 Coyote Fire. The two stands showed contrasting patterns of postfire community composition among different plant groups based on their modes of postfire regeneration. Fire intensity was significantly higher in the older stand. Increased fire intensity was positively correlated with establishment of seedlings of *Ceanothus greggii* var. *perplexans* (an obligate seeder), and negatively correlated with seedling abundance of *Adenostoma fasciculatum* (a facultative seeder). Hillslope position was also important in determining patterns of abundance, suggesting that soil erosion and deposition following fire may have a significant effect on postfire community recovery on these steep sites. Alternatively, prefire differences in the chaparral community that were correlated with hillslope position may account for these differences. The postfire herbaceous community in the first year was dominated by *Phacelia brachyloba*, a fire annual. Contrary to expectations, this species was found in greater abundance in the old stand than in the young. Fire annuals were largely absent from the community in the second year, and were replaced in abundance by a variety of opportunistic native and exotic annuals.

Key Words: *Adenostoma fasciculatum*, chaparral, *Ceanothus greggii*, Coyote Fire, facultative seeder, fire, fire annual, obligate seeder, Sky Oaks Field Station, San Diego County.

Chaparral, an evergreen, sclerophyllous shrubland that dominates in Mediterranean-type climate areas of California, is found in the inland foothills of San Diego County, primarily on steep slopes between 150 and 1400 m elevation. Wildfires are a common feature of the chaparral environment, and the community as a whole is resilient to wildfire (Horton and Kraebel 1955; Hanes 1971; Keeley 1991; Conard and Weise 1998). Chaparral fires are usually stand-replacing crown fires. Vegetation recovery occurs through postfire resprouting from belowground vegetative parts (e.g., root crowns or basal burls; Zedler 1981; Zammit and Zedler 1992) and/or through seedling establishment from soil-stored seeds (Keeley 1986, 2000). Under most burning regimes, community structure is altered only briefly following a burn, and species composition does not change significantly from one fire cycle to the next (Keeley 1991).

Investigating variation in plant groups based on regenerative and/or growth form attributes can provide a link between vegetation responses to disturbance and the effects of these changes on overall community properties and function (Kleyer 1999; Lavorel et al. 1999; McIntyre et al. 1999; Pausas 1999; Guo 2001; Lloret and Vilá 2003; Rusch et al. 2003). California chaparral species show a continuum of postfire regeneration modes from those that regenerate only by resprouting (obligate resprouters) to those that regenerate only from seeds (obligate seeders; Keeley and Zedler 1978; Lavorel et al. 1999; Pausas 1999). Some species are able to both resprout and produce seedlings after fire (facultative seeders; Zedler et al. 1983; Moreno and Oechel 1991a; Beyers and Wakeman 2000; Keeley 2000). Recruitment of new genets of most seeding species is restricted primarily to the first postburn year (Keeley et al. 1981; Moreno and Oechel 1991b; Keeley 2000).

Generally, there is an abundant, but temporary, growth of herbaceous and suffrutescent vegetation in the first several years following a fire. Although short-lived, this initial growth supports high species diversity due to a profusion of postfire annuals. By the third or fourth year, shrubs dominate the site through vigorous resprouting and growth of seedlings (Sweeney 1956; Keeley 1977, 2000; Keeley and Keeley 1986). However, postfire vegetation recovery in any given location is greatly influenced by the varying means of re-establishment of the common species found on the site and in the region, by varying fire regimes (e.g., fire intensity, season,

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frequency and history), and by postburn weather patterns (Keeley et al. 1989; Moreno and Oechel 1994).

In July 2003, the lightning-ignited 9700-ha Coyote Fire swept through San Diego State University's (SDSU) Sky Oaks Field Station (San Diego County, CA), a long-term ecological research site. This study documents the impact of the Coyote Fire, specifically examining the effects of pre-fire stand age, fire intensity, and hillslope position, on patterns of vegetation recovery during the first and second postfire growing seasons in two contrasting stands of mixed chaparral at Sky Oaks. Fire intensity, the amount of heat released per unit of time, is related to fire severity, which is the effect of this heat release on ecosystem properties. A surrogate measure of fire intensity was used to analyze variations in fire severity between the two stands (Bond and van Wilgen 1996). Although chaparral responses to fire are well documented in the literature, monitoring the effects of a naturally-ignited summer wildfire at this long-term research site adds value to decades of observational and experimental studies on fire ecology that have occurred there.

Based on the literature, we expected that: (a) the abundance of fire annuals would decrease in the second postfire year, while the cover of other annuals and shrubs would increase (Keeley et al. 1981, 1985; Keeley and Keeley 1986); (b) fire intensity would be higher in the old stand due to its dense canopy and greater accumulation of fuel (Reid and Oechel 1984; Keeley 2000); (c) the diversity and abundance of herbaceous species would be higher in the young stand due a more recently replenished seed bank (Keeley et al. 1981; Keeley 2000); (d) fire intensity would decrease mature plant survival, resprouting potential, and seedling germination in most shrub species (Moreno and Oechel 1991a; Sparks and Oechel 1993); however, (e) germination of obligate seeding species would be favored by high fire intensity (Rundel et al. 1987; Borchert and Odion 1995); and, (f) patterns of pre-fire shrub densities and postfire erosion across hillslope positions would also likely impact the postfire community (Riggan et al. 1988; Davis et al. 1989; Moreno and Oechel 1991b, Rice 1993).

We addressed three main research questions: (1) Was there a difference in fire intensity between the two stands? (2) How did patterns of postfire vegetation reestablishment differ between stands in the first and second postfire year, and over time? (3) Were any other site-related factors (e.g., pre-fire shrub density, fire intensity, slope inclination, and cover of other plant groups) associated with patterns of postfire vegetation recovery?

Methods

Study Area

Sky Oaks Field Station (33° 21′ N, 116° 34′ W; 1400 m elevation) is located in northeastern San Diego County. The study includes two sites at the Field Station: (1) a young stand with a pre-burn age of 12 yr (resulting from a controlled burn in early spring of 1992), and (2) an old stand with a pre-burn age of approximately 60 yr. The prescribed burn was conducted to reduce fuel and fire hazard around micrometeorological and other instruments at the site, but, unfortunately, detailed records of that fire were lost in the 2003 Coyote fire. Prefire stand age in the old stand was determined using growth rings from three basal stem sections of the obligate seeder *Ceanothus greggii* var. *perplexans* found in an adjacent unburned patch (Keeley 1992, 1993; nomenclature follows Hickman 1993, authorities given in Table 1).

Sky Oaks was completely consumed in the Coyote Fire, which burned under hot, dry, and windy conditions. Sites were selected in an effort to minimize variability in all environmental factors except stand age. The two stands were less than 0.5 km apart, both at the same elevation and on a west-to-southwest facing slope, with slope gradients ranging between 23–29° at high hillslope positions and 9–18° at low hillslope positions. The prefire chaparral community was co-dominated by *Adenostoma fasciculatum* and *Ceanothus greggii* var. *perplexans* (Moreno and Oechel 1991a).

Mean annual precipitation at the field station is 381 mm, the majority falling between November and March (average based on unpublished data from 1994 to 2003, Sky Oaks Weather Station, SDSU Global Change Research Group). For the first precipitation year following the fire (September 2003 to August 2004), precipitation was below average, particularly in the spring of 2004. However, precipitation during the second postfire season was well above average from October 2004 through February 2005 (Fig. 1).

Data Collection

Data were collected in spring of 2004 and 2005 during the first and second post-fire growing seasons. Vegetation was sampled along three parallel 150-m transects permanently established within each stand. Transects were arranged perpendicular to the slope about 50 m apart at high-, mid- and low-hillslope positions in order to account for the effects of postfire erosion and deposition (Keeley et al. 2005a). Permanent sampling plots, each 1.0-m^2 with a 0.25-m^2 subplot, were arranged randomly within each 5-m segment of transect. This design yielded 30

TABLE 1.   PLANT SPECIES FOUND IN THIS STUDY, ARRANGED BY PLANT GROUP. OS = obligate seeder; FS = facultative seeder; OR = obligate resprouter; FA = fire annual; OA = opportunistic annual; FP = fire perennial, E = exotic; Other = not assigned a group or included in analyses (because of a very low Importance Value). References for plant group designations: Keeley et al. 1981; Zedler 1981; Zedler et al. 1983; Keeley 1986; Keeley and Keeley 1986; Keeley 1991; Moreno and Oechel 1991a; Zedler 1995a; Keeley and Fotheringham 1998; Keeley 2000. Plant vouchers deposited at San Diego State University Herbarium (SDSU).

Group	Species	Family	Life form
OS	*Ceanothus greggii* A. Gray var. *perplexans* (Trel.) Jepson	Rhamnaceae	shrub
FS	*Adenostoma fasciculatum* Hook. & Arn.	Rosaceae	shrub
OR	*Adenostoma sparsifolium* Torrey	Rosaceae	shrub
	Quercus berberidifolia Liebm.	Fagaceae	shrub
FA	*Antirrhinum coulterianum* Benth.	Scrophulariaceae	herb
	Emmenanthe penduliflora Benth. var. *penduliflora*	Hydrophyllaceae	herb
	Phacelia brachyloba (Benth.) A. Gray	Hydrophyllaceae	herb
	Phacelia minor (Harvey) Thell.	Hydrophyllaceae	herb
OA	*Calyptridium monandrum* Nutt.	Portulacaceae	herb
	Camissonia hirtella (E. Greene) Raven	Onagraceae	herb
	Caulanthus heterophyllus (Nutt.) Payson var. *heterophyllus*	Brassicaceae	herb
	Chaenactis artemisiifolia (A. Gray) A. Gray	Asteraceae	herb
	Cryptantha intermedia (A. Gray) E. Greene	Boraginaceae	herb
	Cryptantha muricata (Hook. & Arn.) Nelson & J.F. Macbr.	Boraginaceae	herb
	Filago californica Nutt.	Asteraceae	herb
	Gilia australis (H. Mason & A.D. Grant) V. Grant & A.D. Grant	Polemoniaceae	herb
	Lotus strigosus (Nutt.) E. Greene	Fabaceae	herb
	Mimulus brevipes Benth.	Scrophulariaceae	herb
	Nemacladus ramosissimus Nutt.	Campanulaceae	herb
	Salvia columbariae Benth.	Lamiaceae	herb
FP	*Eriophyllum confertiflorum* (DC.) A. Gray var. *confertiflorum*	Asteraceae	suffrutescent
	Lotus scoparius (Nutt.) Ottley var. *scoparius*	Fabaceae	suffrutescent
	Penstemon centranthifolius (Benth.) Benth.	Scrophulariaceae	suffrutescent
	Penstemon spectabilis Thurber var. *spectabilis*	Scrophulariaceae	suffrutescent
	Turricula parryi (A. Gray) J.F. Macbr.	Hydrophyllaceae	suffrutescent
E	*Bromus madritensis* L. subsp. *rubens* (L.) Husnot	Poaceae	herb
	Bromus tectorum L.	Poaceae	herb
	Erodium cicutarium (L.) L'Hér.	Geraniaceae	herb
	Hordeum murinum L. subsp. *leporinum* (Link) Arcang.	Poaceae	herb
Other	*Dichelostemma capitatum* Alph. Wood subsp. *Capitatum*	Liliaceae	geophyte
	Orobanche fasciculata Nutt.	Orobanchaceae	herb
	Pellaea mucronata (D. Eaton) D. Eaton var. *mucronata*	Pteridaceae	fern
	Solanum umbelliferum Eschsch.	Solanaceae	suffrutescent
	Vulpia octoflora (Walter) Rydb. var. *octoflora*	Poaceae	herb
	Yucca whipplei Torrey	Liliaceae	suffrutescent

sampling plots per hillslope position per stand, and 90 plots per stand (see Schmalbach 2005 for details).

Measurements of herbs and shrub seedlings were made in the 0.25-m² sampling plots, and measurements of re-sprouting shrubs and dead stumps were made in the encompassing 1.0-m² plots (size based on Moreno and Oechel 1992). The number of shrub seedlings was counted, cover for each species visually estimated by two observers and averaged, and slope gradient (inclination) recorded within each plot using a clinometer. A measure of fire intensity for each sampling plot was estimated from the diameter of the smallest stem remaining on the shrub skeleton of a re-sprouting *Adenostoma fasciculatum* locat-

ed nearest the center of each 1.0-m² plot (Moreno and Oechel 1989; Keeley et al. 2005b). Prefire shrub densities in each stand were estimated postfire using dead and resprouting stumps (Keeley et al. 2005b).

For analysis, plant species were grouped by life form, origin (native, exotic), and mode of regeneration following fire. This yielded seven functional groups: obligate seeder shrub, facultative seeder shrub, obligate resprouter shrub, fire annual, opportunistic native annual, fire perennial, and exotic annual (Table 1). For the obligate seeder and facultative seeder groups, *Ceanothus greggii* and *Adenostoma fasciculatum* (respectively) were the only shrub species recorded. Mortality of seedlings was estimated by
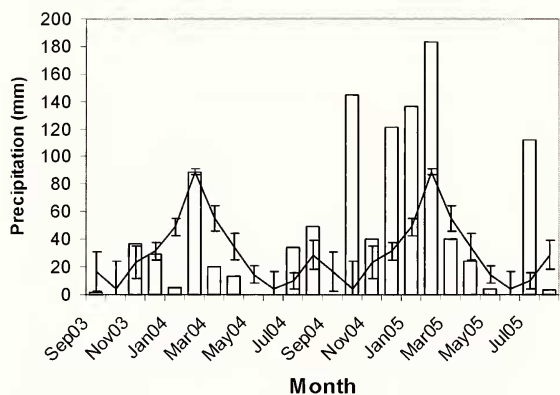
FIG. 1. Monthly precipitation at Sky Oaks Field Station for the first two precipitation years following the Coyote Fire, Sept. 2003–Aug. 2005. Line shows average precipitation per month based on the years 1994–2002. Error bars based on 1 SE. Data for Sept. and Oct. 2003 are from the Western Regional Climate Center, Oak Grove RAWS; all other data are from the Sky Oaks Weather Station.

the net change in number of seedlings from the first to second postfire year.

Data Analyses

An exploratory analysis of the data from the first postfire season (April 2004) was conducted to determine if spatial dependence was present in the dataset using spatial autocorrelation analysis (Moran's I; Legendre 1993; Almeida-Neto and Lewinsohn 2004). To test for differences in community recovery between the first and second postfire years, a repeated measures analysis of variance (Gurevitch and Chester 1986) was used for each plant group.

Minimum diameter was used for all analyses involving fire intensity as a factor, and it was log transformed to meet normality and heteroscedasticity assumptions. A two-sample t-test was used to determine if fire intensity differed significantly between the old and young stand. One-way ANOVAs were used to test for differences in fire intensity between hillslope positions for each stand. Two-way ANOVAs with the Bonferroni post hoc test for differences between factors were used to compare patterns of recovery between the two stands in the first and second postfire year. To incorporate the potential effects of postfire erosion and deposition, hillslope position was also included as a factor. Finally, relationships between plant group abundance and site-related variables at the plot scale were tested for significance by multiple regression analysis (backward stepwise, $P > 0.15$ to eliminate). All regressions were bootstrapped to verify their stability (statistics were calculated with SYSTAT 10.2).
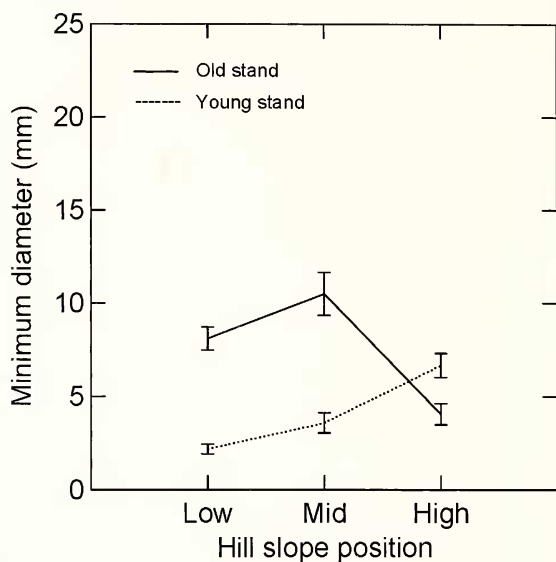

FIG. 2. Differences in fire intensity (shown as average minimum branch diameter) across hillslope positions within each stand. Error bars = 1 SE.

Due to normality and heteroscedasticity issues with both density and cover values, a relative importance value was calculated for each plant group and used in the analyses. The importance value is a weighted average of relative density, relative cover, and relative frequency (calculated per transect) for each species (Jongman et al. 1995). Importance values for each plant group were calculated by summing the relative importance values for each species within that group.

RESULTS

Spatial dependence was present only at a distance of less than or equal to 2 m ($P < 0.01$), considerably less than the average distance between sampling plots (5 m); 13% of the total sampling plots were less than or equal to 2 m apart. Consequently, observations at the sampling plots were treated as independent in all statistical analyses.

Fire Intensity

Fire intensity was significantly higher (e.g., minimum stem diameter larger) in the old stand (7 ± 5.0 mm; mean $\pm$ SD) than in the young stand (4 ± 3.3 mm; $t_{177} = 5.48$, $P < 0.001$). In the old stand, fire intensity decreased from the low to the high hillslope position. In the young stand, the pattern was opposite (Fig. 2).

Postfire Vegetation Comparisons Between Stands

First postfire year. Ceanothus greggii seedlings were significantly more abundant in the old

Table 2.   Effects of Stand (Old, Young) and Hillslope Position (High, Mid, Low) on Functional Group Relative Abundance (Importance Value) Based on Two-Way ANOVA for Selected Plant Groups in 2004 and 2005. F-statistics (p-value) given. (seedl = seedlings; respr = resprouts; both = seedlings + resprouts).

Factor	d.f.	OS	FS seedl	FS respr	FA	OA	E
2004							
Stand	1	492.7 (<0.001)	2.2 (0.139)	0.3 (0.582)	7.3 (0.008)	1012.9 (<0.001)	–
Hillslope	2	10.7 (<0.001)	8.1 (<0.001)	15.8 (<0.001)	4.8 (0.010)	35.5 (<0.001)	–
Stand × Hillslope	2	16.4 (<0.001)	37.7 (<0.001)	1.4 (0.245)	5.6 (0.004)	9.1 (<0.001)	–
2005							
Stand	1	519.4 (<0.001)	14.6 (<0.001)	15.6 (<0.001)	1043.4 (<0.001)	2021.1 (<0.001)	990.9 (<0.001)
Hillslope	2	20.0 (<0.001)	54.1 (<0.001)	28.0 (<0.001)	77.1 (<0.001)	628.7 (<0.001)	42.4 (<0.001)
Stand × Hillslope	2	9.1 (<0.001)	41.5 (<0.001)	0.9 (0.405)	115.4 (<0.001)	38.8 (<0.001)	11.3 (<0.001)

stand, particularly at higher hillslope positions, in the first postfire season (Table 2; Fig. 3a). The relative abundance of *Adenostoma fasciculatum*, in contrast, was most related to hillslope position (Table 2). Abundances of seedlings and resprouting shrubs did not differ significantly between stands (Fig. 3b, c). In the old stand, *A. fasciculatum* seedlings were most abundant lower or higher on the slope, while in the young stand, seedling densities increased with slope steepness (Fig. 3b). The relative abundance of *A. fasciculatum* resprouts was lowest at the low hillslope position within both stands (Fig. 3c). Densities of obligate resprouters, *Adenostoma sparsifolium* and *Quercus berberidifolia*, were too low to be analyzed (seven and three individuals, respectively).

Fire annuals (Table 1) were found in greatest abundance in the old stand primarily due to their abundance at the high hillslope position (Fig. 3d). *Phacelia brachyloba* was by far the most common fire annual species (98% of functional group density and 97% of cover in the first postfire year). Its very low abundance in the young stand at the high hillslope position appears to be the main reason for the difference between stands. Otherwise, abundance was similar across stands and hillslope positions. In contrast, opportunistic annuals (Table 1) were much more abundant in the young stand (Fig. 3e). Their relative abundance increased higher on the slope, especially in the old stand. Fire perennials (Table 1) were relatively uncommon in the first postfire year, present only as seedlings. Abundances were significantly higher in the young stand (Fig. 4), and varied with hillslope position.

Second postfire year. Relative abundances of *Ceanothus greggii* seedlings remained greatest in the old stand, and at mid hillslope positions in the second postfire year (Fig. 3a), in spite of higher seedling mortality there (noted above). In the second year, *Adenostoma fasciculatum* seedlings

were slightly more abundant in the young stand and higher on the slopes (Fig. 3b).

Fire annual cover decreased dramatically in the second postfire year (Fig. 4), and *Phacelia brachyloba* became much less common than other fire annuals (its average functional group importance value decreased from 47% in 2004 to 0.2% in 2005). In the old stand, the density of fire annuals decreased by 74% and cover by 89%, and declines were even greater in the young stand (83% and 97% respectively). Abundance of fire annuals remained greatest in the old stand at the high hillslope position (Fig. 3d). Density of opportunistic native annuals, on the other hand, was 24 times greater in the second postfire year. Relative abundance remained greater in the young stand, and at high hillslope positions (Fig. 3e). The most common opportunistic annual was *Cryptantha muricata* (functional group importance value increased from zero in 2004 to 61% in 2005). Although uncommon in the first postfire year, exotic (non-native) annuals also increased significantly in the second postfire year (Fig. 4), especially low on the slope (Fig. 3f) and in the young stand.

Abundance of fire perennials increased (59%) from the first to second postfire year (Fig. 4). Two new species, *Penstemon spectabilis* and *Turricula parryi*, were recorded that had not been seen the first year. Relative abundance of fire perennials remained higher in the young stand and at high hillslope positions (not shown).

Variation in postfire recovery over time. While there was a decrease in the relative abundance of shrub seedlings in both stands between 2004 and 2005, seedling cover increased for both species (Fig. 4). *Ceanothus greggii* (obligate seeder) seedling mortality was greater in the old stand (37.1%) than in the young stand (12.1%), and differed with hillslope position within each stand (Fig. 5). Establishment of new seedlings in the second postfire year was negligible. In contrast, mortality among *Adenostoma fasciculatum* (fac-
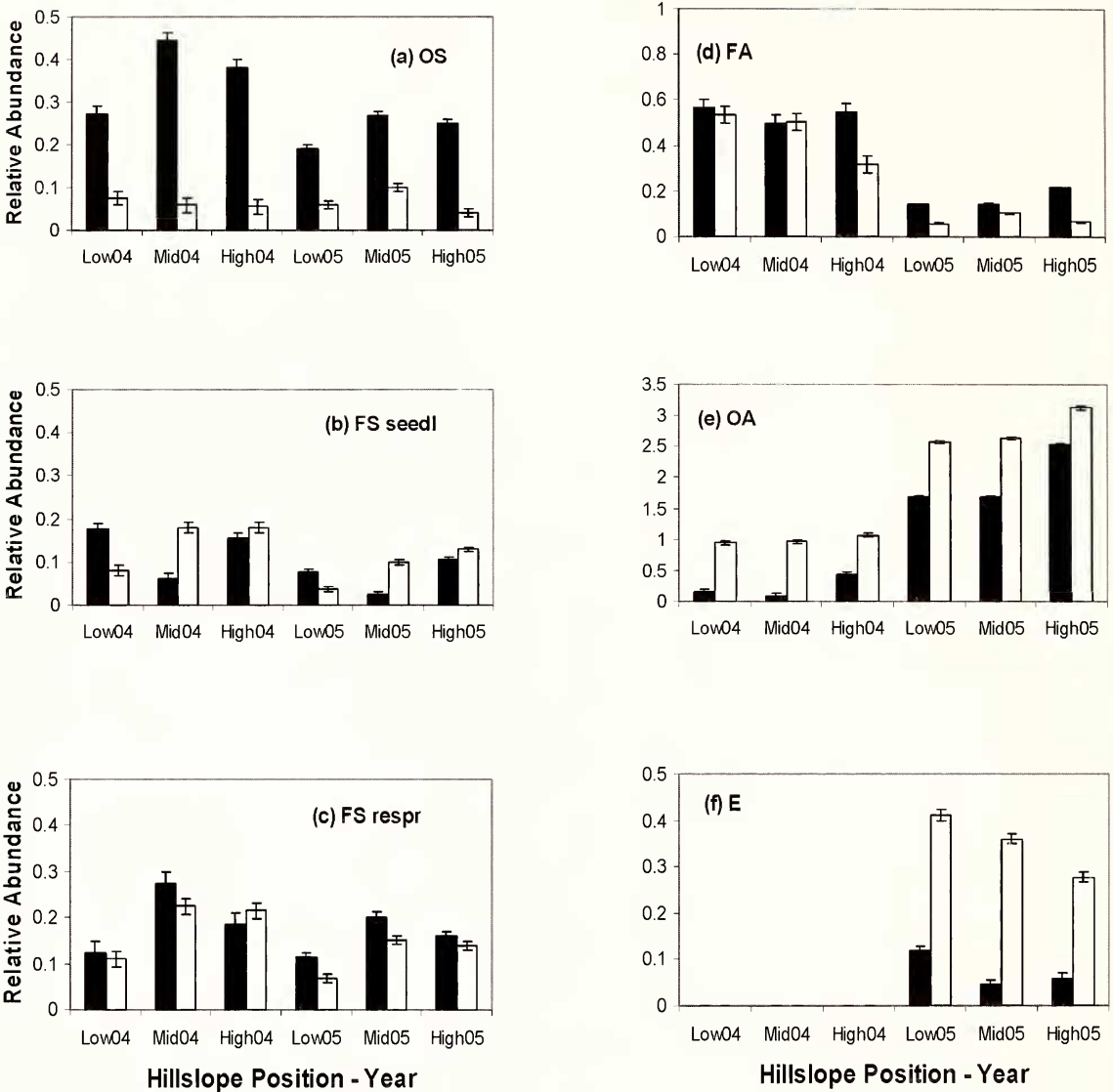
FIG. 3. Relative abundance (average importance value) of plant groups by hillslope position (Low, Mid, High) in the young and old stands for the first (04 = 2004) and second (05 = 2005): postfire seasons (black bar = old stand, white bar = young stand): (a) *C. greggii* seedlings, (b) *A. fasciculatum* seedlings, (c) *A. fasciculatum* resprouts, (d) fire annuals, (e) opportunistic annuals, and (f) exotic annuals. Note varying y-axis. Error bars = 1 SE.

ultative seeder) seedlings did not differ significantly between the two stands (Table 3), although greater mortality occurred low on the slope in both stands (Fig. 5). Cover of *A. fasciculatum* resprouts increased to the same degree in both stands and across all hillslope positions (Fig. 4); however, the relative abundance of resprouts decreased slightly in the young stand in the second postfire year as a result of other functional types increasing in abundance (Fig. 3).

The most striking difference in the herbaceous community between 2004 and 2005 was the disappearance of fire annuals in the second

postfire year (Fig. 4). In contrast, there was a significant increase in the abundance of opportunistic annuals across both stands, most pronounced at the high hillslope position (Fig. 3). Exotic annuals also increased, although not as much in the old stand as in the young (Fig. 4), and in both stands abundances were highest on the low-slope position (Table 3; Fig. 3).

Spatial Patterns in Postfire Recovery at the Plot Scale

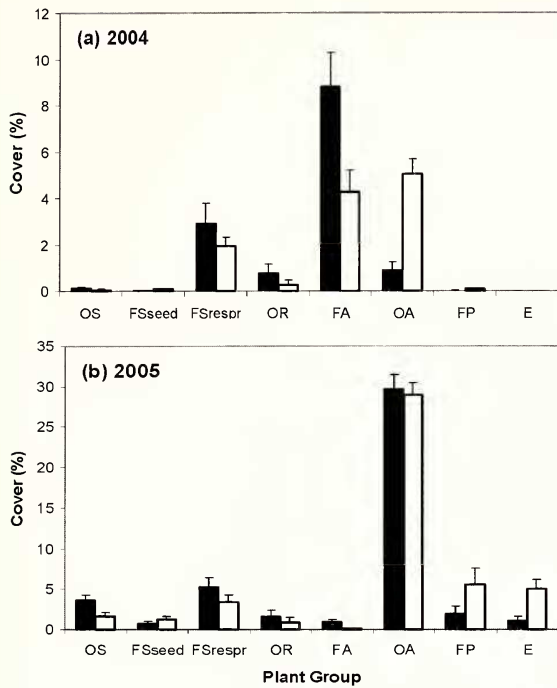*First postfire year.* Data from each stand were analyzed separately given that patterns of postfire

FIG. 4.   Cover for each plant group by stand age (black bars = old stand, white bars = young stand) for a) first (2004), and b) second (2005) postfire year (see Table 1 for definitions of plant groups). FS group split into seedlings and resprouting shrubs. Note varying range of y-axis. Error bars = 1 SE.

recovery differed between the two stands (Table 3). In the old stand, *Ceanothus greggii* (OS) seedlings were more abundant in plots on steep slopes, with higher fire intensity, and low prefire shrub densities (Table 4). In the young stand, slope was the only significant factor affecting plot-level abundance, with more seedlings found on flatter plots (which tend to occur lower on the hillslope). In contrast, more *Adenostoma fasciculatum* (FS) seedlings were found in low fire intensity areas and on flatter locations within the old stand, and where the incline was greater in the young stand (Table 4). None of the site factors
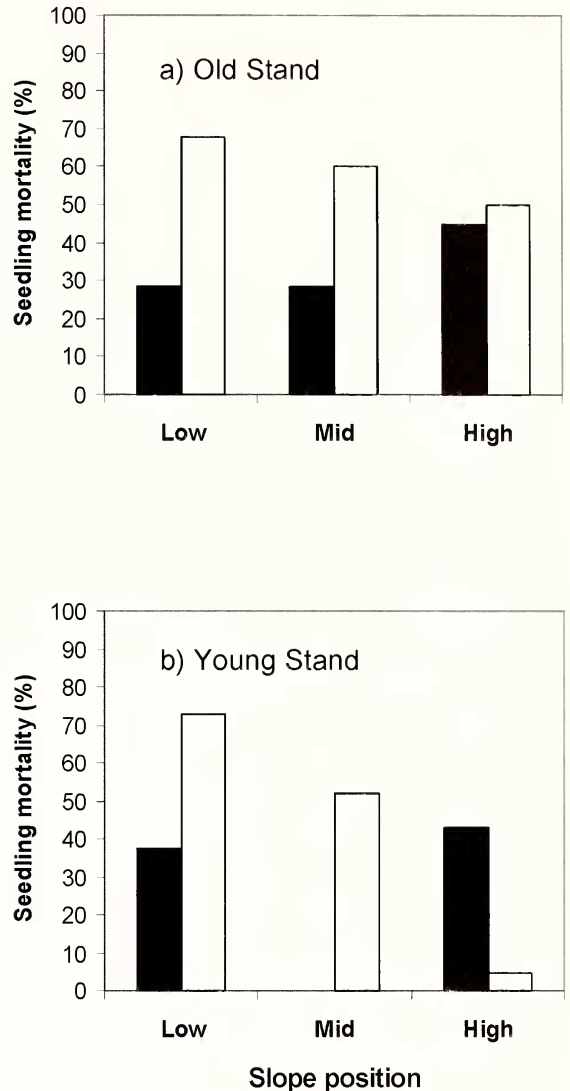

FIG. 5.   Shrub seedling mortality as percent fewer individuals per hillslope position between the first and second postfire year for the (a) old stand and (b) young stand. Black bar = *Ceanothus greggii*, white bar = *Adenostoma fasciculatum*.

TABLE 3.   EFFECTS OF YEAR (2004, 2005), STAND (OLD, YOUNG) AND HILLSLOPE POSITION (HIGH, MID, LOW) ON PLANT GROUP RELATIVE ABUNDANCE (IMPORTANCE VALUE) BASED ON REPEATED MEASURES ANOVA. F-statistics (p-values) given. Plant groups as in Table 1 (seedl = seedlings; respr = resprouts).

Factor	d.f.	OS	FS seedl	FS respr	FA	OA	E
Year	1	107.0 ($<$0.001)	170.0 ($<$0.001)	38.6 ($<$0.001)	594.0 ($<$0.001)	13300.0 ($<$0.001)	3370.0 ($<$0.001)
Year $\times$ Stand	1	116.0 ($<$0.001)	0.3 (0.611)	2.8 (0.094)	0.1 (0.806)	2.7 (0.102)	1390.0 ($<$0.001)
Year $\times$ Hillslope	2	1.6 (0.208)	1.7 (0.191)	2.8 (0.064)	9.1 ($<$0.001)	104.0 ($<$0.001)	58.8 ($<$0.001)
Year $\times$ Stand $\times$ Hillslope	2	12.5 ($<$0.001)	10.1 ($<$0.001)	0.8 (0.438)	2.1 (0.123)	2.0 (0.142)	10.9 ($<$0.001)

TABLE 4. REGRESSION ANALYSIS OF IMPORTANCE VALUES OF PLANT GROUPS (AS IN TABLE 1) VS. SITE PARAMETERS FOR: A) THE FIRST AND B) SECOND POSTFIRE YEARS. Shown is the t-value/coefficient for each factor if $P < 0.05$; *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$; n = 90.

a) Variable	Year 1				
	OS old	OS young	FS old	FS young	FA young
Slope	2.949/0.010**	−2.277/−0.002*	−2.497/−0.005*	5.294/0.008***	−3.544/−0.013***
Fire intensity	2.800/0.164**		−3.474/−0.112***		
Shrub density	−2.213/−0.079*				−2.093/−0.121*
OA cover					−2.341/−0.007*

b) Variable	Year 2				
	OS young	OA old	OA young	E old	E young
Slope		8.646/0.057***	9.040/0.031***	−3.120/−0.003**	−2.020/−0.004*
Fire intensity		−3.572/−0.403***	2.830/0.225**		−3.033/−0.114
Shrub density			−3.230/−0.165**	2.619/0.039*	
OA cover	−2.968/−0.001**				−2.434/−0.002*
OS cover		−2.550/−0.012*	−2.796/−0.009**		
FP cover			−3.942/−0.004***		
E cover			−4.252/−0.006***		
FS cover				−2.113/−0.001*	

significantly affected the distribution of fire annuals in the old stand, while their cover was negatively related to slope, prefire shrub density and cover of opportunistic annuals in the young stand.

Second postfire year. In the young stand, abundance of *Ceanothus greggii* seedlings was negatively related to dense cover of opportunistic annuals in the second year (Table 4). Prefire shrub density and/or cover of other functional groups was negatively correlated with the abundance of opportunistic annuals (OA) in the young stand. The effect of fire intensity on OA was negative in the old stand, but positive in the young, but probably because OA were abundant at high hillslope position (Fig. 3e) where fire intensity differed between stands (Fig. 2). In the old stand, exotics were found in greater abundance on flatter plots where cover of facultative seeder resprouts was less and prefire shrub densities greater. Abundances in the young stand were also greatest on flatter areas where the cover of other annuals was sparse and fire intensity was low (Table 4).

DISCUSSION

Different fire regimes and fire characteristics tend to favor particular plant species based on their mode of regeneration following a fire, and by doing so affect patterns of postfire community composition (Haidinger and Keeley 1993). Variations in soil heating, in particular, can greatly affect recruitment because seeds have different tolerances to heat and different requirements for germination (Keeley and Keeley 1981; Keeley et al. 1985; Zammit and Zedler 1988; Zedler 1995a; Odion and Davis 2000; Le Fer and Parker 2005).

Consequently, postfire recovery patterns among different plant groups are likely to be strongly influenced by fire intensity, and other factors affected by stand age (Moreno and Oechel 1994; Tyler 1995). We found important differences in regeneration patterns between the old and the young stand among the various plant groups.

Fire intensity during the Coyote Fire was higher in the old stand, corresponding to a difference in pre-fire shrub densities, which were also higher in the old stand. Fire intensity was negatively correlated with hillslope position in the old stand, but positively in the young stand. These patterns did not correspond to differences in prefire shrub densities among hillslope positions and may be related to variations in fire behavior or the pattern of burning during the 2003 Coyote Fire, which are unknown.

Mature obligate seeders (e.g., *Ceanothus greggii*) are killed by fire, and recovery of the population depends on the fire-cued germination of seed that have accumulated in the soil over time (Keeley and Zedler 1978; Zedler 1981). Although it has been hypothesized that seed banks may diminish in mature stands of chaparral, there is little evidence of seed bank decline in stands younger than 80-years of age (Keeley 1977; Zammit and Zedler 1988, 1992; Keeley et al. 1989). The old stand at Sky Oaks was estimated to be approximately 60-years old prior to the Coyote Fire, and sustained a mass recruitment of *C. greggii* seedlings in the first postfire season ($12.4 \pm 1.6 \ m^{-2}$; mean $\pm$ SD). Seedling recruitment was lower ($1.6 \pm 0.5 \ m^{-2}$) in the young stand (12-years old), suggesting that *C. greggii* — which requires up to 25 yr to replenish its seed bank (Keeley 1986) — did not accumulate as large a seed bank in this stand during the shorter interval between fires. Further, fire in-

tensity during the 1992 prescribed fire and/or the 2003 Coyote Fire may not have been sufficient to stimulate much germination in this stand (Le Fer and Parker 2005).

In contrast, *Adenostoma fasciculatum* both resprouts and reestablishes from fire-cued germination following a burn, and is generally more resilient to recurrent fires in terms of seedling recruitment (Zedler 1981, 1995b; Moreno and Oechel 1993). Our data are consistent with this in that the abundance of *A. fasciculatum* seedlings did not differ significantly between stands in the first postfire year (old stand $= 2.6 \pm 0.7$ m^{-2}, mean $\pm$ SD; young stand $= 2.7 \pm 0.5$ m^{-2}). As also found in previous studies, however, fire intensity had a significant effect on patterns of establishment (Moreno and Oechel 1991a; Davis et al. 1989). *Adenostoma fasciculatum* seedlings were more abundant in areas with less intense fire, while *C. greggii* abundance was positively correlated with fire intensity.

Seedlings of both species suffered significant mortality between the first and second postfire years. Previous research has found that seedling mortality is strongly related to soil moisture levels during the first six months following germination (Moreno and Oechel 1992). *Ceanothus greggii* mortality was greatest at the high hillslope positions within each stand, where soil moisture levels were probably lower due to steep inclines (Meentemeyer et al. 2001). *Adenostoma fasciculatum* seedlings did not suffer greater mortality at high hillslope positions, however, even though these seedlings have been found to be more sensitive to drying of the soil than *C. greggii* seedlings (Moreno and Oechel 1988, 1992). Herbivory by small mammals is also an important source of mortality and can greatly affect patterns of seedling establishment in the postfire community (Mills 1986; Mills and Kummerow 1989). Overall, *C. greggii* seedlings had a higher rate of survival overall than *A. fasciculatum* seedlings. Recruitment of new seedlings in the second year was negligible, most likely due to a lack of second year germination and/or increased competition from resprouters and already established plants (Keeley 2000; Quintana et al. 2004).

There was no evidence that high fire intensity, over the range of values observed, negatively affected resprouting success in the first postfire year, as has been reported in other studies (Malanson and O'Leary 1985; Rundel et al. 1987; Moreno and Oechel 1991b; Borchert and Odion 1995). Resprout cover increased in the second postfire year in both stands and across all hillslope positions. However, the density and frequency of *A. fasciculatum* resprouts decreased in the young stand between the first and second postfire years. One possible explanation is that energy reserves for resprouting in the young stand, when compared to the old stand, were reduced by the prescribed burn in 1992 and as a result were insufficient to support some of the resprouting shrubs through the second postfire year (Moreno and Oechel 1991b, 1993).

Fire annuals were the most conspicuous herbaceous component of the burn area in the first postfire season, and then virtually disappeared from the landscape in the second year. They arise from a dormant seedbank that is only stimulated to germinate by charred wood, smoke, or heat shock (Keeley et al. 1981, 1985; Keeley and Keeley 1986; Moreno and Oechel 1991a). Contrary to expectations, fire annuals were found in greater abundance in the old stand, where fire intensity was greater, than in the young stand where the prescribed fire that took place 12 years prior to the Coyote Fire was expected to have replenished the seed bank (Keeley et al. 1981; Keeley 2000). Lower germination of fire annuals in the young stand may have resulted from: a) seed bank depletion due to reduced fire intensity during the 1992 controlled burn, reducing the density of seed available for germination after the 2003 fire; b) reduced fire intensity during the 2003 fire, which failed to stimulate germination; and/or c) greater mortality of seeds under moist soil conditions, such as those perhaps present during the spring-time controlled burn in 1992 (Beadle 1940; Sweeney 1956; Le Fer and Parker 2005). Postfire erosion following the 1992 and/or 2003 fires may further explain why fire annuals were least abundant at the high hillslope position in the young stand.

Opportunistic annuals occur in openings in mature chaparral and are common in the early postfire seasons (Keeley et al. 2005a). They have a polymorphic seed bank that contains both non-refractory (opportunistic) and refractory (enhanced germination after fire) seeds (Keeley et al. 1981). While fire annuals were more abundant in the old stand in the first postfire year, opportunistic annuals were more abundant in the young stand where fire intensity was lower. Other studies have also found a negative relationship between the abundance of herbaceous species and fire intensity (Moreno and Oechel 1991a; Keeley 2000). The abundance of opportunistic annuals increased dramatically in the second postfire season, making up 88% of the total herbaceous cover in the old stand, and 73% in the young stand. This was also a year with above average precipitation.

Herbs are generally absent beneath the mature chaparral canopy, but common as seedlings after fire through the enhanced fire-cued germination of soil-stored seed (Keeley et al. 1981; Keeley 2000). Fire perennials were found in greatest abundance in the young stand, perhaps because fire intensity was lower, or because mature plants were still present in the community following the

1992 prescribed burn (Keeley et al. 1981; Keeley 2000).

Seeds of exotic annuals have low residence time in the soil, thus the presence of these species on burn sites is primarily due to postburn colonization. Most, such as species of *Bromus* and *Erodium*, disperse prior to the summer fire season. As a result, they are less common in the first postfire year but present in subsequent years (Keeley 2000), as was seen at Sky Oaks after the Coyote Fire. Exotics were found in significantly greater abundance in the young stand. However, this could be a result of the proximity of the young stand to the field station office area and instrument sites — an area of high human traffic — rather than a consequence of stand age. Abundances were also highest at the low hillslope positions within each stand, and then decreased farther up hill. This pattern may indicate that exotics are dispersing from the office area and access road (which runs along the base of the slope).

Summary

In general, postfire succession in the two mixed chaparral stands at Sky Oaks has been following the general model of chaparral succession as described by other investigators (Horton and Kraebel 1955; Sweeney 1956; Hanes 1971; Keeley 1977; Keeley et al. 1981; Keeley 2000). However, the fire history of a specific site also creates a "legacy effect" (Foster et al. 1998), resulting from the interval, season, and behavior (e.g., prescribed vs. natural; Le Fer and Parker 2005) of the previous fires, which can affect patterns of postfire recovery through future fire cycles. This may have management implications for spring burning in chaparral. Our finding of significantly lower abundance of fire annuals in the young stand illustrates the potentially negative impact to postfire species diversity that may result from reduced fire intensity and altered germination behavior following spring burning.

Based on our findings, the following can be concluded regarding the patterns of postfire vegetation recovery in the two stands at Sky Oaks:

(1) As expected, fire intensity was significantly greater in the older chaparral stand. Variation in fire intensity significantly affected patterns of postfire regeneration in several plant groups.

(2) There were significant differences between stands in the patterns of reestablishment for all plant groups during the first and/or second postfire year. Many differences were as predicted given the relative age of, and fire intensity differences between, the stands.

(3) Other site-related variables, however, were also associated with patterns of postfire vegetation reestablishment, in particular hillslope position and prefire shrub density. The effects of hillslope position suggest that factors such as prefire species patterns, soil moisture, nutrient dynamics, and erosion and deposition play a role in the postfire patterns of most plant groups. Spatial patterns found in the abundance of each plant group in relation to changes in prefire shrub density imply that a landscape of different-aged stands burning at varying intervals may lead to enhanced biodiversity in chaparral.

Our ability to infer the causes of the observed patterns is limited by the lack of spatial replication, but this is a common problem in disturbance ecology (there was only one Coyote Fire, and only one southwest-facing hillslope at Sky Oaks). However, the future value of this study may lie in continued monitoring at this permanent research site, which could complement extensive regional surveys (e.g., Keeley et al. 2005a). In particular, we predict that the abundance of exotic herbaceous species will decline as the shrub canopy closes at the field station. This may also serve as an important reference site for comparison with the very large area of southern California that burned a few months later in the October 2003 fire storm, much of that area in the wildland-urban interface (Moritz et al. 2004).

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